

POPULATION DYNAMICS OF ROSS'S GEESE

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In this chapter, we estimate annual rates of change for Ross's goose populations, and evaluate population response to increases in harvest. This exercise requires estimates of fecundity and survival and is based largely on unpublished data and analyses in progress (Alisauskas et al. ms^a, Alisauskas et al. ms^b), or unpublished progress reports (Alisauskas et al. 1998b) based on ongoing research. Some estimates of vital rates (e.g., breeding propensity) for Ross's geese were not available and are the object of current research. It must be stressed that this modeling exercise is an approximation and makes a number of assumptions that are detailed below. In some cases, these reflect our attempt to simplify a complex system while in others it reflects uncertainty in the population parameter estimates. Current uncertainty regarding some parameters required that assumptions be made about specific probabilities, based on information on other Arctic goose populations or our best estimates. In cases where data were absent for Ross's geese, we relied on data from other species. In cases where we were uncertain about appropriate parameter values, we used values in population projection matrices that would result in an underestimation of the Ross's goose growth rate. Thus, our conclusions are subject to future revision as new information becomes available, and should be considered as preliminary.

Background

Under density-independence, population size in any year, N_{t+1} , is a function of size in the previous year, N_t , times the finite rate of population change or annual rate of population growth, λ , simply

$$N_{t+1} = \lambda N_t$$

So, for declining populations, $\lambda < 1$; if the population is stable, $\lambda = 1$; and if the population is increasing, $\lambda > 1$. Further, λ can be estimated from age-specific survival and fecundity rates using Leslie projection matrices (see below), but in its simplest form,

$$\lambda = F + S$$

where F = some measure of recruitment per female and S = annual survival rate of adult females (see below). The annual rate of population growth can also be estimated by log-linear regression of N over t (e.g., Eberhardt and Simmons 1992) as

$$\log N_t = \log N_0 + t \log \lambda$$

where $\log \lambda = e^r$ for continuously breeding populations or, alternatively and more appropriately for Arctic goose populations, $\lambda = (1 + r)$, and r is the intrinsic rate of increase (i.e., the population growth rate per individual).

Realized Growth in Population of Breeders at Karrak Lake

According to current estimates, more than 90% of Ross's geese still spend much of the summer in their traditional nesting areas in the Queen Maud Gulf Bird Sanctuary (QMGBS), despite some expansion of breeding range to the west and east (Ryder and Alisauskas 1995). Alisauskas et al. (1998) visited 87 of 92 light goose colonies documented by Kerbes (1994) and Alisauskas and Boyd (1994); 74 of these were active colonies. The 5 largest colonies contained over 92% of nesting geese in or near QMGBS. These 5 colonies (including Karrak Lake) also accounted for 91% of Ross's geese in the region. The Karrak Lake colony alone contained 40% of Ross's geese in the region. Kerbes (1994) estimated that Karrak Lake contained 38% of known Ross's geese near Queen Maud Gulf (QMG) in 1988. The number of Ross's geese nesting at Karrak Lake, together with its central location in the QMG, suggests that this colony well represents the continental population of breeding Ross's geese. Kerbes (1994) estimated from photographic counts of geese at known colonies that the average finite rate of increase in Ross's geese at QMG during 1965-88 was 1.077.

Since Kerbes' (1994) report, a photo-survey conducted in 1998 estimated 437,837 light geese nesting at Karrak Lake (R. H. Kerbes, personal communication). If all population estimates of Ross's geese from aerial photography (1976-98) and Ryder's estimate from 1965 are used in log-linear regression over time (1965-98), the finite rate of increase is 1.080.

Numbers of breeding Ross's geese have been estimated annually at Karrak Lake, 1993-2000, using stratified sampling of nests on 30-m radius plots. Sample plots were stratified based on nest density and sampling intensity and were systematically spaced at 0.5 km intervals in areas of high nesting density in the center of the colony, or increments of 1 km in areas of lower nest density. Nests were not obstructed by vegetation, and we have assumed complete detection of nests because of high visibility and multiple visits to sample plots. All nests on each plot are mapped and all eggs are measured and counted. Nests of Ross's and lesser snow geese were discriminated using egg measurements following Alisauskas et al. (1998a). Plots are revisited at least once to estimate nest success. Survival rate of individual eggs was estimated by visiting a subsample of nest plots up to 5 times. Standard procedures were followed using estimators in Thompson (1992:103). Breeding population estimates (\hat{N}) and 95% confidence limits (CL) were:

1993: 225,000 \pm 86,000;
1994: 198,000 \pm 62,000;
1995: 224,000 \pm 79,000;
1996: 359,000 \pm 136,000;
1997: 218,000 \pm 79,000;
1998: 329,000 \pm 99,000;
1999: 404,000 \pm 85,000;
2000: 395,000 \pm 106,000.

Regression of $\text{Log}(\hat{N}_t)$ on t , where $t_0 = 1993$, yields $95\%CL(r) = 0.0972 \pm 0.0729$. Following Eberhardt and Simmons (1992), we calculate $\lambda = (1 + r) = 1.0972$, because using $\lambda = e^r = 1.1021$, which implies continuous population growth, is not realistic for "birth pulse" populations such as Arctic-nesting geese. Thus, estimates of realized λ for breeding geese were derived independently from the estimates of λ using population projection (see below).

This point estimate of λ is higher than the one variously estimated for midcontinent lesser snow geese ($\lambda \approx 1.05$) (Rockwell et al. 1997). Interestingly, Ross's geese at Karrak Lake show annual rates of population increase almost twice that of midcontinent lesser snow geese, and this has important implications on the relative potential response of each species to increased harvest rates.

Estimation of Survival Rates

We estimated annual survival probabilities, S , for Ross's geese banded and recovered during 1961-99 using band-recovery models (Brownie et al. 1985) as implemented by Program MARK (White and Burnham 1999). We included all adults banded in North America ($n = 13,083$) regardless of location of banding, as most were banded north of 56°N latitude; juvenile geese were stratified by whether they were banded north of 56°N latitude (summer $n = 12,915$) or south (rest of the annual cycle $n = 2,337$). For this exercise, we used the mean survival rate of adults and young calculated from year-specific survival rates. We estimated process variation in age-specific survival rates using these data following White et al. (in press). Results of survival estimation used in this report are preliminary, but are based on current analyses and preparation of Alisauskas et al. (ms^b)

Modeling Details

We examined population dynamics of Ross's geese with a projection model approach. In brief, we computed the mean 10-year stochastic growth rate from the best available estimates of demographic variables and their variances using brute-force, Monte Carlo modeling. We then used the results to project the continental population of this species for 10 years at the mean growth rate and at the upper and lower 95% confidence limits of that rate. We repeated the exercise using values of some of the variables depreciated by 1% to ascertain the relative impact of such changes on the population's dynamics. Finally, we examined the impact of additional annual removal of adults from additional harvest on population dynamics.

We used a 3-stage model (ages = 1, 2, 3+) to allow for the potential of reduced reproductive success of birds in age class 2. We parameterized it as a pre-breeding census, birth-pulse model where the first row fertilities are:

$$F_i = BP_i \times 0.5 \times CS \times NS \times HS \times GS \times s_0$$

where BP is breeding probability, CS is clutch size, NS is nesting success, HS is hatching success, GS is gosling survival from hatching to fledging and s_0 is juvenile survival from fledging to the next pre-breeding census. We assume that $BP_1=0$ and that $BP_2 \leq BP_{3+}$. We assume that these variables function independently from one another, and from adult survival.

The survival cells ($a_{2,1}$, $a_{3,2}$ and $a_{3,3}$) were all set to s_a . Because variance in these parameters is a biological reality, we used a stochastic approach rather than a deterministic one based solely on means. For stochasticity, we selected estimates for the variables for a single year by drawing them from an appropriate random distribution (below), combined them according to the formulation of a pre-breeding census matrix, projected the population for 1 year, reselected

estimates, projected for the next year, and so on for 10 years. In all cases, we assume stochastic effects are independent of each other. We then calculate the stochastic growth rate for the population λ_s using the Heyde-Cohen (1985) equation:

$$\ln \lambda_s = \frac{\ln N(T) - \ln N(1)}{T-1}$$

To obtain an estimate of the mean and 95% confidence limits of the stochastic growth rate, we repeated this 1000 times and report the arithmetic mean and the lower and upper 2.5 percentiles (i.e., upper and lower 95% CL) of the 1000 estimates.

Owing to the log-normal nature of the distribution of population size, the average of these stochastic growth rates is less than or equal to that obtained by extracting the dominant eigenvalue of the mean matrix (λ_0). This is seen in the relation:

$$\ln \lambda_s = \ln \lambda_0 - \frac{\sigma^2}{2}$$

To place the stochastic growth rates on the usually recognized scale, we exponentiated the mean and the confidence limits. Note that the exponentiated confidence limits are not symmetrical about the exponentiated mean.

For illustrative purposes, the mean and 95% CL's were used to project populations of fixed initial size for the 10-year period and presented as graphs. To examine the relative impact of some potential management options, we re-ran these simulations decrementing either the age-specific survival probabilities or the age-specific fertility estimates by 1%. Because the elements contributing to fertility are multiplicative and independent, decrementing the fertility rates by 1% could represent a 1% decrement in any single element or a composite decrement totaling 1%. We present projections using these decremented stochastic growth rates as graphs for illustrative purposes. We also calculated the relative effect of these perturbations as:

$$re_i = \left(\frac{\lambda_{base} - \lambda_i}{\lambda_{base}} \right) \times \left(\frac{1}{p} \right)$$

where λ_{base} is the unperturbed stochastic growth rate, λ_i is the decremented stochastic growth rate and $p = 0.01$. These values are analogous to elasticities extracted from the mean deterministic matrix but do not necessarily equal them numerically. Like elasticities, however, they provide a guide to the relative impact an equal proportionate change in a demographic variable would have on stochastic growth rate of the population.

Parameter Estimates

Unless otherwise noted, age-specific fertility or survival rates come from papers, reports, or unpublished data of R. T. Alisauskas (cited above). In the following, we detail how point estimates and associated distributions were determined, and how they were incorporated into the stochastic model.

Breeding Propensity: $BP_2 = 0.35$; $BP_{3+} = 0.82$ - no values are available for Ross's geese (ROGO) so we initially used those for lesser snow geese from La Pérouse Bay. Estimates are from Rockwell et al. (1997) with BP_{3+} being an average over the La Pérouse Bay estimates for i

= 3, 4, 5+. This is an area where more information is required for Ross's geese, and which is currently being investigated at Karrak Lake.

Clutch Size: We used data from 1966 to 1999 from Karrak Lake. Mean estimate is 3.49 and the variance is 0.047. The latter reflects both process and sampling variance. Assuming the two are independent, the value represents an upper limit on process variance. Using it will underestimate the stochastic growth rate. We sampled this variable from a random normal distribution using 3.49 and 0.22 as μ and σ (see Tuljapurkar 1997).

Nesting Success: We used data from 1966 to 1999 from Karrak Lake. Mean nesting success was 0.83 with a range of 0.68 to 0.92. We sampled this variable from a random uniform distribution with those lower and upper limits.

Hatching Success: We used data from 1995 to 1998 from Karrak Lake. With only 4 year's data, we used a constant mean value of 0.82.

Gosling Survival: Although there are some data on the immature-to-adult ratios at hatching and near fledging from Karrak Lake, those data do not include an estimate of pairs that suffered total failure because such birds may move out of the sampling area. Thus, the initial trials of the model made use of lesser snow goose data from La Pérouse Bay. Using those data from Rockwell et al. (1997), this variable was estimated as a composite of total brood survival (1-TBF) and gosling survival (P3). We used the means over age classes of 0.93 and 0.69 for a composite of 0.64. This is an area where we require more data.

Juvenile Survival: We used data with a mean of 0.54 and variance of 0.0398 (see above). As for clutch size, the variance is a composite of process and sampling variance. We assumed this variable follows a beta distribution and estimated the shaping variables A and B by simulation in MATLAB release 12. They are $A = 2.834$ and $B = 2.41$. We sampled this variable using those estimates and BETARND from the statistics tool box of MATLAB release 12.

Adult Survival: We used data with a mean of 0.866 and (square root of) process variance of 0.0128 (see above). This estimate predates the special regulations and conservation order associated with the management of lesser snow geese of the Mid-continent Population, and should reflect survival of Ross's geese associated with "normal" harvest. Again, we assumed a beta distribution with shaping variables estimated by simulation of $A = 608.3929$ and $B = 94.156$. Again, we sampled this variable using BETARND.

Results

For reference to population dynamics of Ross's geese before increased harvest of midcontinent lesser snow geese associated with the conservation order, we calculated a deterministic, average matrix based on the means of the fecundity and survival parameters. The deterministic growth rate found as the dominant eigenvalue of the matrix is $\lambda_0 = 1.0926$. The stochastic growth rate of this population is estimated from our modeling as $\lambda_s = 1.0904$ with lower and upper 95% confidence limits of 1.0438 and 1.1343 respectively. As expected, the

stochastic growth rate is less than the deterministic one, but both are very similar to the estimate from log-linear analysis of trend data in estimated population size of Ross’s geese breeding at Karrak Lake, 1993-2000. Projections for a population initialized with 400,000 females are depicted in Fig. 1. This represents projected growth of this population in the absence of any additional harvest associated with special regulations or conservation order periods stemming from the lesser snow goose management program. Fig. 2 represents population size from an initial population of 500,000 females for comparison with Fig. 1.

The growth rate of the population with a 1% reduction in adult survival (maintaining a fixed coefficient of variation) is $\lambda_s = 1.0811$ (1.0355 to 1.1225). This represents a relative reduction in stochastic growth rate of 0.85. For a 1% reduction in fertility, the stochastic growth rate is $\lambda_s = 1.0885$ (1.0425 to 1.1296) corresponding to a relative reduction of 0.17. These relative effects on stochastic growth (0.85 and 0.17) agree reasonably well with the asymptotic elasticities of adult survival and fertility estimated from the deterministic matrix as 0.84 and 0.16, respectively. The relative effects of these reductions are depicted in Fig. 3.

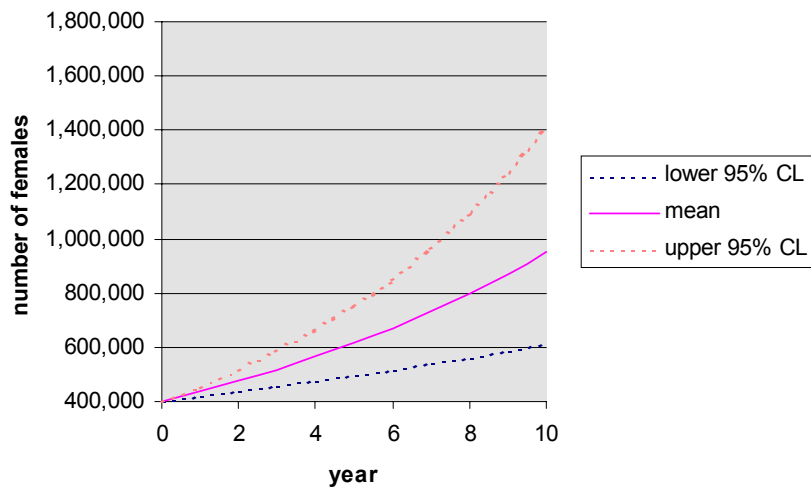


Fig. 1. Stochastic population projection of Ross’s geese over 10 years assuming an initial population size of 400,000 females.

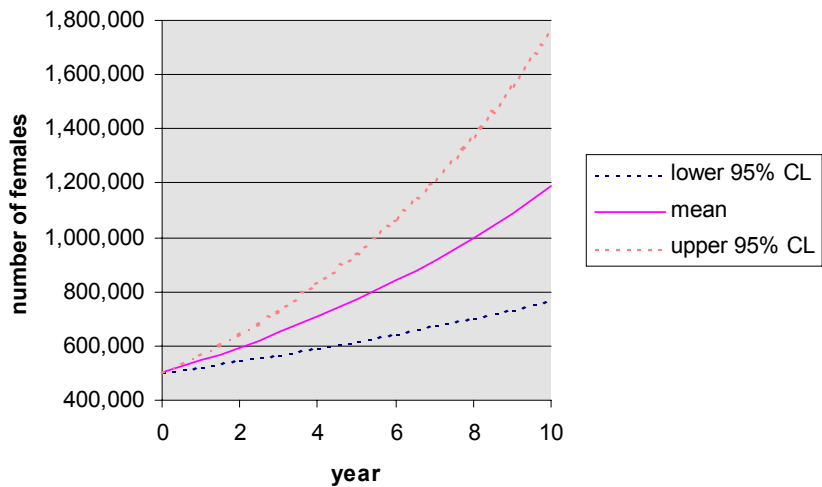


Fig. 2. Stochastic population projection of Ross’s geese over 10 years assuming an initial population size of 500,000 females.

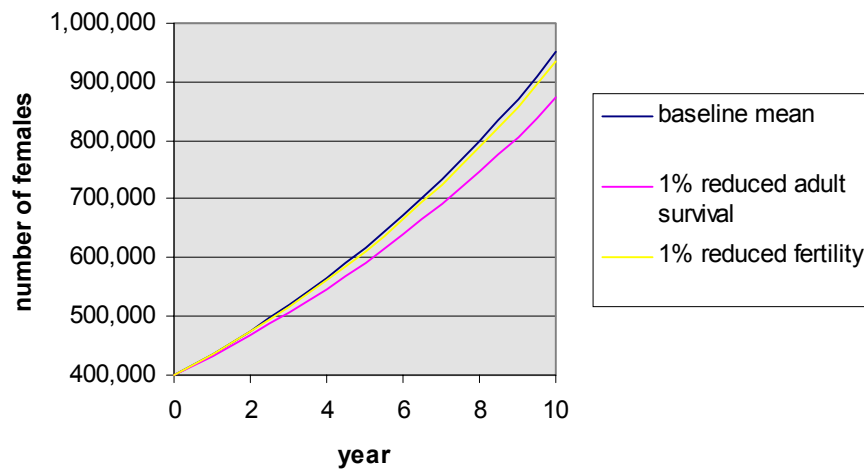


Fig. 3. Relative effects of 1% reduction in adult survival and recruitment on base population growth of Ross’s geese. Initial population size of 400,000 females is assumed.

We estimated the potential impact of additional harvest of Ross’s geese resulting from the expanded lesser snow goose harvest regulations implemented in 1998-99 (refer to harvest chapter) modeling the removal of a fixed number of Ross’s geese each year. This is similar to “by-catch” models used in fisheries projections. We estimated the number of Ross’s geese removed in the following way. For the regular season, we calculated the average total harvest of

Ross's geese in the Central and Mississippi Flyways (U.S.) and Canada for 1995 to 1997, the 3 years before any special regulations were implemented. This total is 40,432. We subtracted that mean from the total for 1999 of 86,665 and considered the difference of 46,233 to be the total Ross's "by-catch" during the regular season.

We estimated Ross's goose harvest during conservation order periods (1998-99 and 1999-2000) from 1999-2000 data, the higher harvest of the 2 years available. During conservation order periods we only have harvest estimates for snow and Ross's geese combined. We assumed that the proportion of Ross's geese in the conservation order harvest was the same as within the Mississippi and Central Flyways during the 1999 regular-season harvest, 0.037 and 0.124, respectively. The 1999-2000 conservation order harvests in those 2 flyways were 362,872 and 238,948, respectively and scaling by the appropriate harvest proportions yields a conservation order Ross's goose harvest of 43,056. The total Ross's goose by-catch is thus 89,289 (i.e., 46,233 + 43,056) and since our model considers only females, we estimated the fixed number of Ross's goose females to be removed as 44,645 (assuming an equal sex ratio in the harvest).

The impact of additional harvest of Ross's geese under the assumption of additive mortality is depicted in Fig. 4 for an initial population of 400,000 females and in Fig. 5 for an initial population of 500,000 females. We examined 2 scenarios. In the first, a constant block of 44,645 was removed each year for all 10 years of the projection. Assuming the true stochastic growth rate of the population is near the estimated mean or below, this scenario leads to a reduction if the initial population size of Ross's geese $<496,000$. This is an extreme scenario, however, since the size of the by-catch is likely to go down as the population declines. Moreover, the removal is not likely to extend for 10 years. Current management scenarios for the midcontinent population of lesser snow geese target a 5-year program. Furthermore, it is important to note that the projection is sensitive to the initial population size, and that populations comprised of $>496,000$ female Ross's geese will not decline at the rate illustrated in Fig. 4, and in fact, continue to increase (Fig. 5).

We examined a second scenario where the increased harvest of Ross's geese was suspended after 5 years. Although the same decline is seen when the actual stochastic growth rate is near the estimated mean or below, the population quickly rebounds when additional harvest was terminated (Fig. 6) on an initial population of 400,000. Again, for initial populations $>496,000$ females, the additional block harvest would not induce population declines (Fig. 7). This may be one of the most important points of this exercise. Given the conservative nature of our estimates of the population growth potential for this species and the nature of this by-catch pressure, it is clear that the species is capable of rebounding in a quick and positive fashion.

It is important to stress that the patterns depicted in both of our scenarios depend heavily on the starting population size estimate of 400,000 females. Given that value and our estimated stochastic growth rate of $\lambda = 1.09$, then an additional block harvest $>36,000$ females will lead to declines as depicted. Viewed in the opposite way, if the size of the "by-catch" is 44,645 and the source population for this extra harvest is really $\geq 496,056$ (rather than 400,000) the mean growth rate, depicted as declining in Fig. 4, would actually increase (Fig. 5). This shows not only how

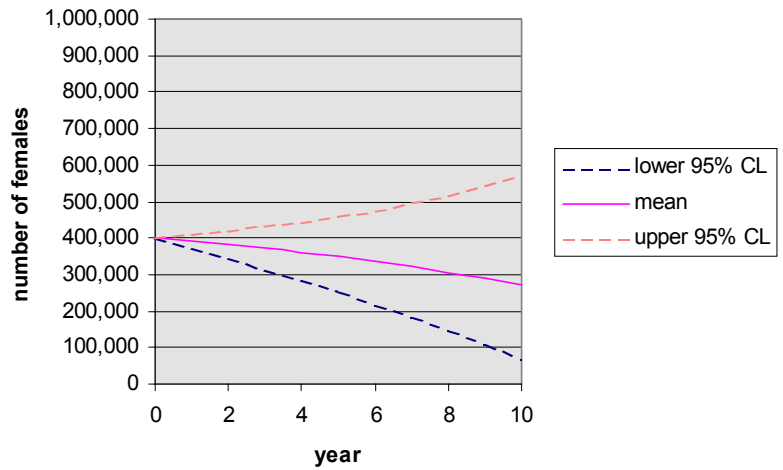


Fig. 4. Effect of additional harvest of 44,645 females on Ross's goose population growth, assuming an initial population of 400,000 females. Initial populations $\geq \sim 496,000$ result in continued population increases at this level of additional harvest.

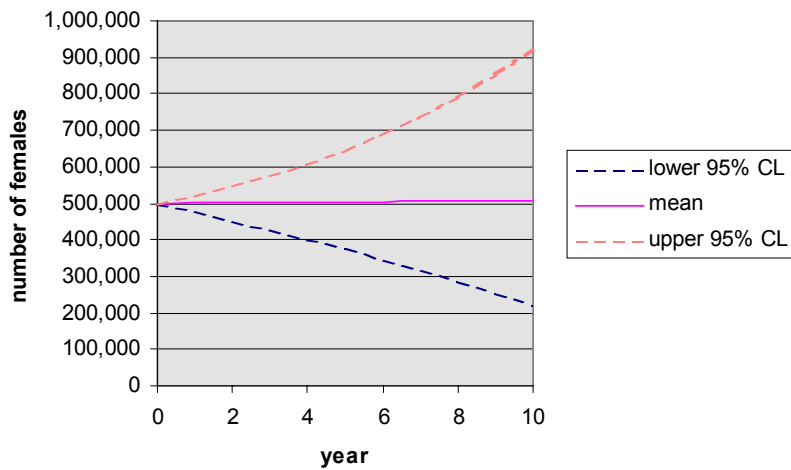


Fig. 5. Effect of additional harvest of 44,645 females on Ross's goose population growth, assuming an initial population of 500,000 females. Initial populations $\geq \sim 496,000$ result in continued population increases at this level of additional harvest.

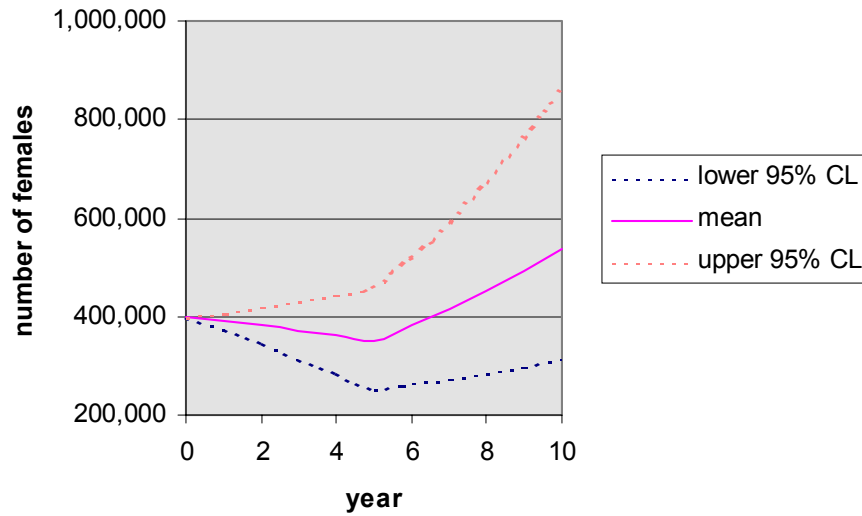


Fig. 6. Effect of additional harvest of 44,645 females for 5 consecutive years on Ross's goose population growth, assuming an initial population of 400,000 females.

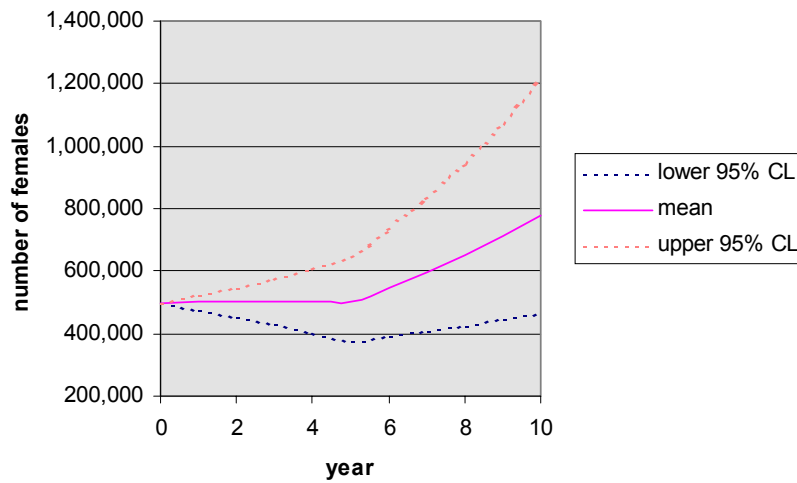


Fig. 7. Effect of additional harvest of 44,645 females for 5 consecutive years on Ross's goose population growth, assuming an initial population of 500,000 females.

sensitive the projections are to initial conditions but emphasizes the need for continued estimation of survival and fertility rates through continued banding and nesting studies.

Other Considerations

Our simulations assume a homogenous population of Ross's geese exposed equally to a base and extra-season harvest rate across their range. However, it is wise to consider historical changes in the numbers and distribution of Ross's geese across North America. Before their eastward expansion in migration and winter range, Ross's geese were largely confined to the Queen Maud Gulf region in Canada's central Arctic during summer, eastern Alberta and western Saskatchewan on the Canadian Prairies during migration, and the Central and Imperial Valleys of California in the Pacific Flyway during winter. Current Ross's goose population levels are at peak historical levels in the Pacific Flyway as well as the newly pioneered areas of the midcontinent (Kelley et al., this report). Thus, conclusions from our modeling exercise about expected reduction in Ross's goose population growth as a result of new regulations for midcontinent snow geese should be thought of as overestimating the effects. Conversely, it could be viewed that the "by-catch" would constitute a larger proportion of the Ross's geese that winter in the midcontinent region. Again, however, such developments might wisely be considered from the historical context of Ross's goose distribution. Even if it were possible to seriously reduce Ross's geese from their range in the recently pioneered midcontinent region, it is expected that Ross's geese in the Pacific Flyway would continue to grow under current conditions. Compared to rarity of Ross's geese in the 1950's (Ryder and Alisauskas 1995), a reduced number in the midcontinent region concurrent with the presence of hundreds of thousands in California probably should not prompt biological concern. Finally, under all of these scenarios of variable population size and bulk additional harvest, the North American population of Ross's geese is predicted to remain above the North American Waterfowl Management Plan population goal of 100,000 breeding geese (or 50,000 breeding females).

Final Caveat

We stress that the results presented are preliminary and based on a lot of assumptions. We strongly urge that estimation of survival and fecundity rates for Ross's geese continue.

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